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Natural History of the Wood Frog (*Rana sylvatica*) in the Shawnee National Forest, Southern Illinois

Michael Redmer

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March 2002

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Michael Redmer is a biologist with the United States Fish and Wildlife Service, Chicago Illinois Field Office. He completed work on this project while a graduate student in the Department of Zoology, Southern Illinois University at Carbondale.

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Introduction

In the past 20 years, a number of studies have documented considerable intraspecific geographic variation in life history traits of wide-ranging amphibians (Augert and Joly 1993; Berven 1982a, 1982b, 1988; Berven and Gill 1983; Dushane and Hutchinson 1944; Hemelaar 1988; Miaud et al. 1999, 2000). Regionally limited studies that provide data on local amphibian populations can also contribute to the understanding of geographic variation in wide-ranging species by providing baseline data necessary to compare various life-history and population characteristics.

Regional studies of amphibian populations may also contribute to the understanding of amphibian declines. Since 1990, reports of such declines from various parts of the world have led to well-publicized concern about amphibian populations (Blaustein 1994; Blaustein and Wake 1995; Wake 1991, 1993; Wyman 1990). An effort to identify research needs and to begin monitoring amphibian populations was started in the early 1990s by the International Union for the Conservation of Nature and Natural Resources (IUCN). The possibility of global decline has been difficult to assess because amphibian populations are known to undergo cycles of increase and decrease (McCoy 1994; Pechmann and Wilbur 1994; Travis 1994). Although amphibian biology is an active field of study, there is a general lack of baseline data against which to measure population changes (Wake 1993), and important population characteristics (i.e., fecundity, demography, longevity, their interrelationships, and phenology) remain poorly understood even for many common species (Duellman and Trueb 1986). Once gathered, such baseline data can be useful for planning long-term study of population characteristics. In addition, documenting vulnerability to decline will require application of methodologies to obtain data on population cycles. Such methods can be best developed and tested on populations of common species not currently undergoing declines.

The wood frog, *Rana sylvatica*, is a small North American ranid characterized by distinct dorsolateral folds; brown, tan, or dark gray coloration; light stripes on the upper lips; and dark masks along the sides of the face (Fig. 1A). Tadpoles have high tail fins, primarily black bodies with scattered iridophores, and light lines along the ventrolateral edges of the head (Fig 1B). The male breeding vocalization is a fast two-note chuckle that can be heard over only short distances. Although its range is primarily boreal, *R. sylvatica* is the most widespread North American amphibian species (Martof 1970). It occurs from the southern Appalachian Mountains of Georgia, north into Canada above the Arctic Circle, and west to Alaska (Conant and Collins 1998; Martof 1970). The western edge of its range runs roughly diagonally from Alaska and the Northwest Territories southeast through eastern North Dakota and other upper midwestern states (Minnesota, Wisconsin, Illinois) to northeastern Alabama. There are disjunct populations in Colorado, Wyoming, and the Ozark Plateau (Conant and Collins 1998; Martof 1970). The range includes much of the eastern region of the continent, which is highly populated by humans. *Rana sylvatica* has been used extensively by ecologists as a study organism. There have been many regional studies of its life history, including populations near the periphery of its range (Camp et al. 1990; Corn and Livo 1989; Davis and Folkerts 1986; Meeks and Nagel 1973; Trauth et al. 1989, 1995). Because of its large geographic distribution and its occurrence in many habitats at a broad range of elevations, significant phenotypic and life history variation has been reported (Berven 1982a, 1982b; Berven and Gill 1983; Martof and Humphries 1959). Throughout most of its range in Illinois, the wood frog has been an uncommonly collected species (Redmer 1998; Smith 1961) and there are few data on its natural history in the state.

I studied several aspects of the natural history and population biology of *R. sylvatica* in the Shawnee National Forest (SNF) between 1993 and 1997. The primary objective was to conduct the first extensive study of this species in Illinois. The first portion of this study documented the distribution of *R. sylvatica* in the SNF. Observations of general aspects of natural history (predation, amphibian commu-

Figure 1A. An adult male *Rana sylvatica* from Jackson County, Illinois.

Figure 1B. Tadpole of *R. sylvatica* from Jackson County, Illinois. Photographs by Michael Redmer.

nity associates, and larval period) were also recorded. I then identified and qualitatively characterized types of breeding ponds and woodland habitats in which the species occurs, and recorded the phenology of breeding activity and weather conditions at which they occurred. I then used skeletochronology to estimate individual ages of wood frogs, and compared statistical correlations between age and body length of individuals and female age and body length with clutch size and ovum size.

Methods

Study Area

This study took place within the boundaries of the United States Forest Service (USFS), Shawnee National Forest (SNF) in southern Illinois, between 1993 and 1997. The SNF is located roughly between 37° and 38° North latitude, and 88° to 100° West longitude.

Distribution

Before 1992, there were few records of *R. sylvatica* from the region (Redmer 1998). To document new localities, searches were conducted during or immediately following the breeding season (late February through early March). Individual vouchers were collected on roads or at breeding ponds. Potential breeding ponds (vernal ponds and flooded depressions) were located by listening for chorus frogs (*Pseudacris feriarum*) and spring peepers (*P. crucifer*) after late winter thaws in February, or by visiting man-made "wildlife ponds" plotted on USFS-SNF topographical maps. During early spring, ponds were inspected for wood frog choruses or searched for the distinctive egg masses or tadpoles. Upon discovery in ponds at new localities, <50 eggs or tadpoles were collected and raised through metamorphosis in the laboratory. All surviving metamorphs were preserved and vouchers were deposited in the Fluid Vertebrate Collection, Department of Zoology, Southern Illinois University at Carbondale (SIUC).

Habitat

Breeding Ponds. Breeding ponds were both natural and human-made. Natural ponds included ephemeral woodland pools (with variable basins, little or no aquatic vegetation, and dried in summer of all years) and semi-permanent ponds (with distinct basins and aquatic vegetation, and dried in some years). Human-made ponds or depressions included flooded roadside ditches, ruts caused by vehicle traffic on earthen or clay-based roads, and wildlife ponds. Maximum depth (to the nearest cm) of breeding ponds was measured with a meter stick while egg masses were still present.

Terrestrial Habitat. Terrestrial habitats around breeding ponds or wherever else *R. sylvatica* was collected were floodplain or upland forest, classified on the basis of published plant community descriptions (Voigt and Mohlenbrock 1964). Dominant species of trees and other general observations on vegetative cover were recorded. Canopies over ponds were classified as closed (> 75% canopy cover after leaf-out) or open (< 75% canopy after leaf-out).

Population Studies

A population of *R. sylvatica* in southern Jackson County (37°39'N, 89°04'W) was studied intensively between 1993 and 1997. This population bred in at least 12 breeding pools or ponds in Cave Creek floodplain 1–1.5 km N of Pomona and another pond along an arm of Cedar Lake ca. 1.8 km E of Pomona and 2.5 km ESE of the center of the Cave Creek area.

Breeding Phenology. Oviposition dates at the Cave Creek floodplain were recorded from 1993 through 1997 and at Cedar Lake from 1995 through 1997. From 1994 through 1997, weather conditions at the center of the Cave Creek study site were monitored every 24 h from 1 February until at least one week after secession of breeding activity. Minimum-maximum thermometers (VWH Scientific) were mounted on a stake 0.2 m above ground, and buried 5–10 cm below the soil surface. Mean daily temperatures were calculated by averaging daily minimum and maximum air and soil temperatures. Precipitation (to the nearest 0.1 cm) was measured with a scientific rain gauge (Productive Alternatives, Inc.,

Fergus Falls, MN). Correlations between minimum-maximum air and soil temperatures were determined by bivariate regression analyses. Oviposition dates were plotted against trends in weather variables in an attempt to determine whether wood frog emergence and breeding behavior followed consistent annual patterns during this study.

Demography. The ages of 188 individuals were estimated by skeletochronology. Skeletochronology allows estimation of individual age from the number of annular lines of arrested growth (LAGs) on cross-sectioned diaphyses of long bones such as femora or phalanges. This method has proven effective in seasonally variable climates where growth is greatly reduced or prevented by low winter temperatures (Halliday and Verrell 1988). Studies on post-release mortality of toe-clipped amphibians are few, but generally show an insignificant reduction in survivorship (Clarke 1972; Ott and Scott 1999; Reaser and Dexter 1996). Thus, skeletochronology is a relatively harmless method with which to sample age within anuran populations. This technique has been popular in Europe for nearly 20 years and appears (based on increasing publications) to have gained increased use in North America since 1986 (Bastien and LeClair 1992; Redmer 1999). In most studies, amputated toes were preserved, cross-sectioned, stained with hematoxylin, and periosteal LAGs were counted under a microscope. The total number of LAGs (more intensely stained lines) indicates the number of winter dormancies through which an individual has lived. Since endosteal bone growth can cause resorbtion and remodeling of the periosteal bone cortex (and thus obliteration of some periosteal LAGs), application of statistical methods to estimate loss of periosteal LAG has been recommended (Hemelaar 1985; Sagor et al. 1998).

In this study, most (n = 172) wood frogs were collected during 26–28 February and 3–6 March 1995. Eight amplexed pairs were collected on 5 March 1996. The sample consisted of 119 males and 69 females, of which 139 (93 M:46 F) were from Cedar Lake and 49 (26 M:23 F) were from Cave Creek. Frogs were collected by hand, with a dipnet, or with 36-cm-tall nylon drift-fence/funnel trap arrays erected along parts of the margins of three Cave Creek ponds.

Captured frogs were transported to the laboratory in insulated coolers (naturally amplexed pairs were kept together in plastic bags separate from individuals). In the laboratory, sexes and snout-vent lengths (SVL; measured with a plastic ruler to the nearest 1.0 mm) were recorded and each individual was assigned a unique number. The fourth toe of one hind foot of each frog was amputated at or below the joint between the penultimate and third phalanges and fixed for at least 24 h in 10% formalin, rinsed in running tap water for 12 h, and stored in 70% ethanol. Most frogs were returned within 12 h to the place of capture. Twenty-four gravid females were euthanized by immersion in 20% ethanol, fixed in 10% formalin, stored in 70% ethanol, and dissected later for counts of oviductal eggs. Amplexed pairs were kept together in glass bowls in the laboratory for 24–48 h to allow oviposition and all resultant egg masses were preserved in 5% formalin so counts and measurements of pre-yolk plug embryos could be made later.

Glass-mounted cross-sections of phalanges were prepared. Each preserved toe was defleshed manually and the penultimate phalanx from each separated from the others. The penultimate phalanges were decalcified in Kristensen's formic acid solution for 6 h and rinsed for 24 h in running tap water. After initial decalcification, bones were dehydrated automatically (V.I.P.® Tissue-Tek machine), infiltrated with paraffin, embedded individually in paraffin blocks, and cross-sectioned at 10 µm with a microtome. Some bones found to be brittle when sectioned were decalcified further at the tissue face for 15 min in RAPID® nitric acid solution. Ten to 30 mid-diaphysial cross-sections of each bone were attached with adhesive gelatin to microscope slides. Sections then were cleared, hydrated, stained, and dehydrated by immersion in the following sequence of solutions and reagents: (1) three baths, 3 min each in Histoclear; (2) two baths, 2 min each in 100% ETOH; (3) 2 min in 95% ETOH; (4) 10 sec in distilled

water; (5) 15 min in Shandon® instant regressive hematoxylin; (6) 10 sec in distilled water; (7) two dips, 1 sec each, in acid ETOH; (8) 1 min in $LiCO_3$; (9) two baths, 2 min each, in 100% ETOH; and (10) two baths, 2 min each, in 100% ISOH. Processed sections were mounted in Permont® mounting medium under glass cover slips.

Bone cross-sections were interpreted by the procedures and criteria of previous skeletochronology studies (Castanet and Smirina 1990; Castanet et al. 1993; Hemelaar 1985; Hota 1994; Sagor et al. 1998; Smirina 1994). Diameters of bone characteristics were measured at 160X to the nearest 5 µm with a calibrated ocular micrometer mounted in a binocular compound microscope. From the medullary cavity (MC) to the exterior, the bone layers are metamorphosis line (ML), endosteal bone (EB), and subsequent lines of arrested growth (LAGs) in cortical periosteal bone. ML and EB were not always present. Because bone cross-sections were oval or irregular in outline, their diameters were calculated as the square root of the product of the greatest diameter and the greatest diameter perpendicular to it as suggested by Hemelaar (1985) and Sagor et al. (1998).

Because remodeling was detected in some bone samples, age estimates were made as follows. If metamorphosis lines were present, or if endosteal and periosteal LAGs were present in a 1:1 ratio, age was estimated by counting periosteal LAGs (each LAG = 1 yr). Because tissues were collected from frogs that had just emerged from hibernation, the LAG deposited during the winter was not discernible from the outer bone perimeter; thus, the outer perimeter was counted as a LAG. In some instances, EB was broken or absent (as evidenced by resorbtion patterns in periosteal bone layers), probably because of damage caused by the microtome blade. In these instances, the diameter of the space where MC and EB had been was recorded as the diameter of EB. To determine what percentage of early LAGs may have been obliterated by endosteal bone growth, I compared the mean diameter of endosteal bone with mean diameters of the innermost and second visible LAGs. If the diameter of the endosteal region was $\geq$ 2 SD more than the group mean, LAG 1 was considered to be resorbed, and the innermost LAG was counted as LAG 2. If only part of a LAG was obscured by endosteal bone remodeling, the area of endosteal bone was calculated. If it was > 2 SD smaller than the mean of the next LAG, the partial visible LAG was counted as LAG 1. Estimated age was compared to SVL for both males and females using bivariate regression analyses.

Clutch Size. Preserved gravid females were dissected and oviductal ova were removed from egg envelopes. Diameters of 10 ova from each clutch were measured to the nearest 0.05 mm with a calibrated ocular micrometer mounted in a binocular dissecting microscope. Because most preserved ova were aspherical, average diameter was recorded as the square root of the longest axis multiplied by the longest axis perpendicular to it. Females that spawned in the laboratory as well as their spawned eggs and any eggs remaining in the oviducts were preserved. Ova and pre-yolk plug-stage embryos were counted and 10 from each clutch were measured as above. Clutches in which embryos developed past the yolk-plug stage were not included in these analyses because such embryos can achieve diameters significantly larger than those of earlier developmental stages (Rugh 1948; Kaplan 1979).

Other Natural History Notes

Observations of predation, associations with other amphibians, larval periods of 22 cohorts (from wild-collected eggs raised in the lab), and the dates metamorphosed frogs were first observed in the wild also were recorded.

Data Analyses

All statistical analyses were made with StatView® (Abacus Concepts, Inc.) version 4.5 software for Windows. Two-tailed *t*-tests were used to test for differences between age and size distributions. Bivariate regression analysis was used to calculate correlations between the following variables: (1) age and SVL, by sex; (2) age and fecundity; (3) SVL and fecundity; and (4) fecundity and mean ovum diameter. Descriptive statistics such as

sample size (N), range, mean, squared product moment coefficient (r^2), standard errors (SE), standard deviation (SD), degrees of freedom (df), and *t* values (*t*), were calculated as appropriate. All alpha levels were set at < 0.05.

Results

Distribution

Wood frogs were found at 20 localities within the SNF (Redmer 1998; Fig. 2). All localities were in the Shawnee Hills and Ozark Natural Divisions (Schwegman 1973) in Jackson (8), Union (4), Hardin (1), Pope (6), and Saline (1) counties. No wood frogs were found in the central portion of the SNF (Johnson and Williamson counties), Alexander County, or in the Cretaceous Hills Section of the Coastal Plain Natural Division in Massac, Pulaski, and southern Pope counties despite extensive searches (Redmer 1998).

Habitat

Breeding Ponds. Thirty ponds or flooded depressions in which oviposition was observed were at or near 18 of the documented localities. Of these, 21 (70%) were natural, and 9 (30%) were human-made or modified. Natural ponds included 14 (47%) ephemeral pools, 6 (20%) semi-permanent ponds, and 1 (3%) depression in a grassy field. Human-made or modified ponds included four (13%) flooded tire ruts, three (10%) wildlife ponds, and two (7%) roadside ditches. All oviposition sites were lentic. Although most (70%) ponds were in floodplains and thus may have been subject to periodic flooding (and invasion by fishes) from nearby streams, fishes (*Gambusia affinis*, *Fundulus* sp.) were observed in only three (10%) semi-permanent ponds. Twenty-one (70%) breeding ponds were under closed canopies, eight (27%) were under open canopies, and one (3%) was in a field about 50 m from mesic forest. Ponds were variable in

Figure 2. Distribution of *Rana sylvatica* in the Shawnee National Forest, southern Illinois. Solid circles indicate localities confirmed by the author. The triangles indicate the locations within the Pomona study site (Cave Creek and Cedar Lake) mentioned in the text.

size, depth, and shape. Ephemeral woodland ponds with egg masses present were 22–78 cm (mean = 41 cm) deep. Semi-permanent ponds were 60–95 cm (mean = 74 cm) deep, tire-ruts 10–40 cm (mean = 24 cm) deep, and roadside ditches 40 and 60 cm (mean = 50 cm) deep. Wildlife ponds were 40–90 cm (mean = 60 cm) deep, and the flooded grassy field was 65 cm deep.

Terrestrial Habitat. Twenty-one (70%) breeding ponds were in upland floodplains (the valleys of second- or third-order streams) and nine (30%) were on hills or ridges. In the western part of the SNF (Jackson and Union counties), 21 (91%) ponds were in floodplains and 2 (9%) were in uplands. In the eastern part of the SNF (Pope and Hardin counties), six (85%) ponds were in uplands (on ridges) and one (15%) was in a floodplain.

The localities of *R. sylvatica* in the SNF were associated with mixed mature and second growth deciduous forest at six (30%) localities, mature deciduous forest at seven (35%), mixed deciduous and planted pine (*Pinus* sp.) at five (25%), and monotypic planted conifer groves at two (10%) localities, both in Pope County. Trees most frequently noted in the mature deciduous forests included beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), tulip poplar (*Liriodendron tulipifera*), American elm (*Ulmus americana*), sweet gum (*Liquidambar stryaciflua*), and sycamore (*Platanus occidentalis*). This composition indicates a community intermediate between moist lowland and ravine forests as described by Voigt and Mohlenbrock (1964), but scattered red bud (*Cercis americanus*) and flowering dogwood (*Cornus florida*), as well as lush ephemeral herbaceous cover, indicated greater similarity to the latter one. Mixed mature-second growth woodlands were primarily in floodplains and usually not far from mature forest. Several trees (especially *A. saccharum* and *L. tulipifera*) occurred in thickets of box elders (*A. negundo*) and green ash (*Fraxinus lanceolata*), often with dense patches of cane (*Arundinaria gigantea*) and the vines poison ivy (*Rhus radicans*) and catbriar (*Smilax* sp.). Mixed deciduous-coniferous forests usually included canopies of pine (primarily *Pinus taeda*) along with *F. lanceolata, A. negundo, A. saccharum, L. tulipifera*, oaks (*Quercus* spp.), and hickories (*Carya* spp.). The ground where *R. sylvatica* occurred in two planted *Pinus* groves was covered by mats of needles and little vegetation other than abundant *R. radicans* and patches of club moss (*Diphasiatrum digitatum*).

In systematic searches through areas where *R. sylvatica* was known to occur, adults were rarely encountered after the breeding season. I observed seven alive on roads at night, and two during the day in shallow leaf litter near the bases of overhanging bluffs. All were found in April in forested ravines or valleys with plant communities similar to those described above.

Population Studies

Breeding Phenology. *Rana sylvatica* breeding activities (chorusing and oviposition) were explosive. Few males were heard calling and no amplexed pairs were found during daylight hours. In all years, a few males called one or two nights before oviposition was observed, and egg masses were found only after nights when numerous males called. The first dates of breeding activity were as follows: 17 March (1993), 19 February (1994), 27 February (1995), 26 February (1996), and 22 February (1997). The mean date of the onset of breeding activity was 26 February, and the mean date when breeding activity occurred was 28 February. At both Pomona-area study sites, oviposition took place over two to six nights (mean = 4) per year, but was not observed to occur more than two nights in any one pond. The peak of chorusing and oviposition was not always on the same night in neighboring ponds, and the breeding season throughout the study site usually lasted longer than it did in individual ponds.

Breeding activity took place after several days of warming air and soil temperatures (Figs. 3–5). Mean air and mean soil temperatures were highly correlated ($r^2 = 0.72$, $P < 0.001$, $df = 148$) before, during, and after the breeding seasons of 1994–1997. The minimum/maximum surface air temperatures on the dates of first oviposition were -1/21°C (1994), 4/19°C (1995), 6/22°C (1996), and 10/

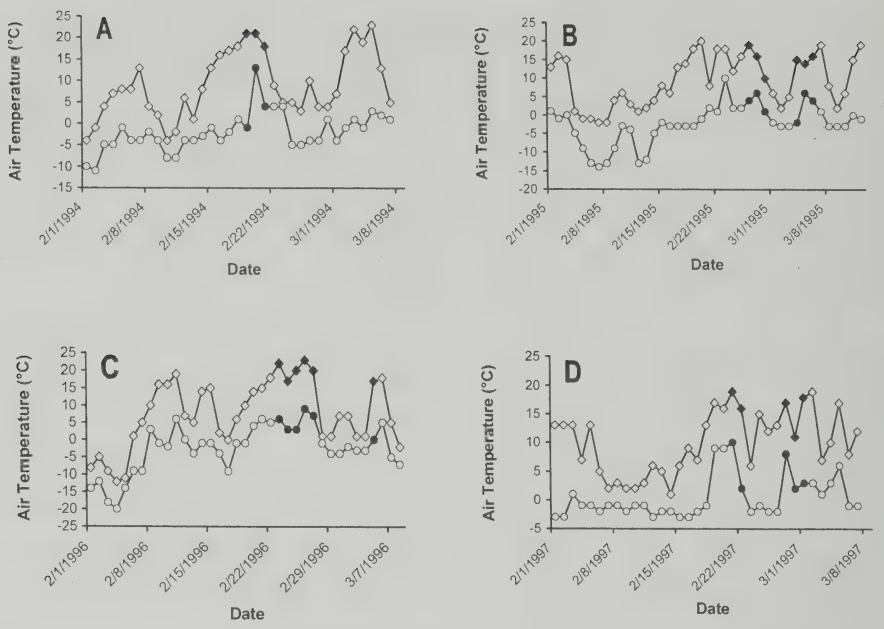


Figure 3. Daily minimum (circles) and maximum (diamonds) surface-air temperatures prior to, during, and immediately following spawning of *Rana sylvatica* at the Pomona/Cave Creek study site, southern Jackson County, Illinois, in the years (A) 1994, (B) 1995, (C) 1996, and (D) 1997. Solid symbols indicate dates when oviposition occurred.

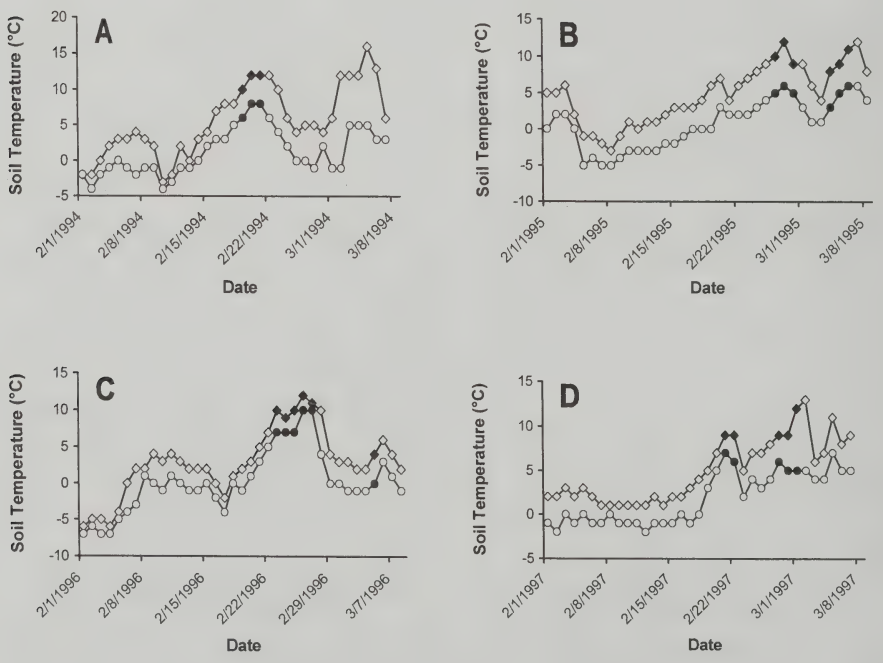


Figure 4. Daily minimum (circles) and maximum (diamonds) soil temperatures prior to, during, and immediately following spawning of *Rana sylvatica* at the Pomona/Cave Creek study site, southern Jackson County, Illinois, in the years (A) 1994, (B) 1995, (C) 1996, and (D) 1997. Solid symbols indicate dates when oviposition occurred.

19°C (1997). Minimum/maximum soil temperatures on these dates were 6/10°C (1994), 5/10°C (1995), 7/10°C (1996), and 7/9°C (1997). From 1994 through 1997, the onset of breeding occurred only after days when mean soil temperatures first reached 7.5°C and maximum soil temperature first reached 9°C. Breeding began during or within 24 h following a rain event only in 1997 (Fig. 6). In 1995, 1996, and 1997, breeding was interrupted by cold fronts that brought lower air temperatures (maximums <10°C, minimums <0°C) and resumed after temperatures rewarmed (Fig. 3). In 1993 breeding activity (which lasted only two nights) did not begin until March 17. Apparently it was delayed by unseasonably low temperatures and heavy snowfalls in late February and early March. In 1994, 1995, and 1996, post-oviposition drops in air temperature caused surface water (and eggs near the surface) to freeze. In these cases, egg masses inspected after subsequent thawing contained some live, developing embryos.

Demography and Skeletochronology. Hematoxylinophilic LAGs (Fig. 7) were detected in all phalangeal cross-sections except those from five (3%) first-year males. There was overlap in the diameters of all bone characteristics but mean diameters did not overlap between sequential characteristics (Table 1). Metamorphosis lines were found in 12 (6%) specimens. In 21 (11%), endosteal bone remodeling was extensive enough that it encroached over periosteal bone and partially obliterated LAG 1. In seven (4%), the diameter of the endosteal bone was <1 SD less than the mean for all complete LAG 1 and the first visible LAGs had diameters within the range of LAG 2s. In these seven, it is likely that endosteal bone growth completely obliterated LAG 1, and the innermost LAGs represented LAG 2. In the 21 remaining specimens with partially obliterated LAG, the diameters of endosteal bone growth between 1–2 SD less than the mean diameter of all LAGs 1 indicated that the partial LAG was LAG 1.

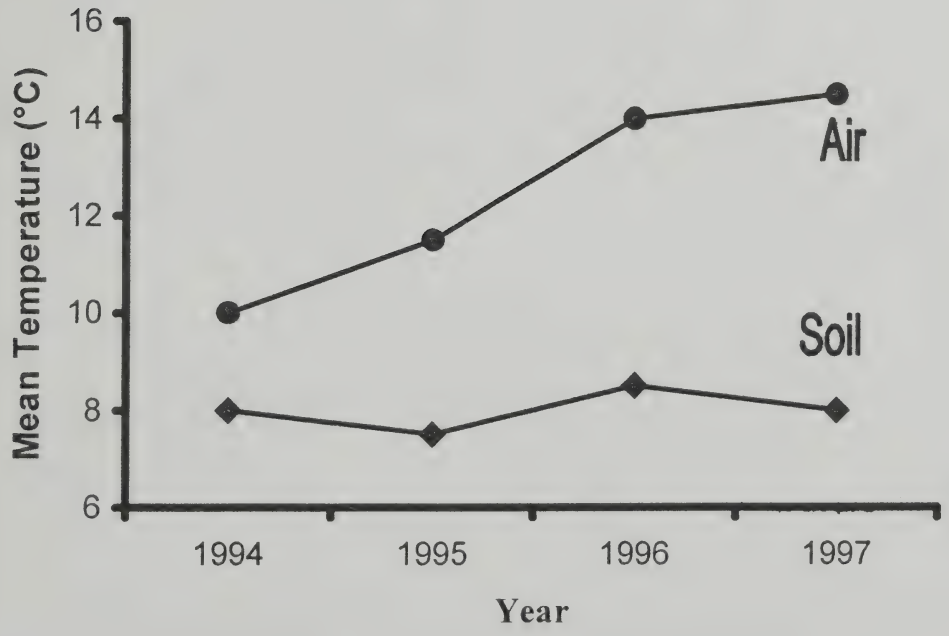


Figure 5. Mean air (circles) and soil temperatures (diamonds) during 24-h periods preceding the onset of breeding activity by *Rana sylvatica* in the vicinity of Pomona, Jackson County, Illinois.

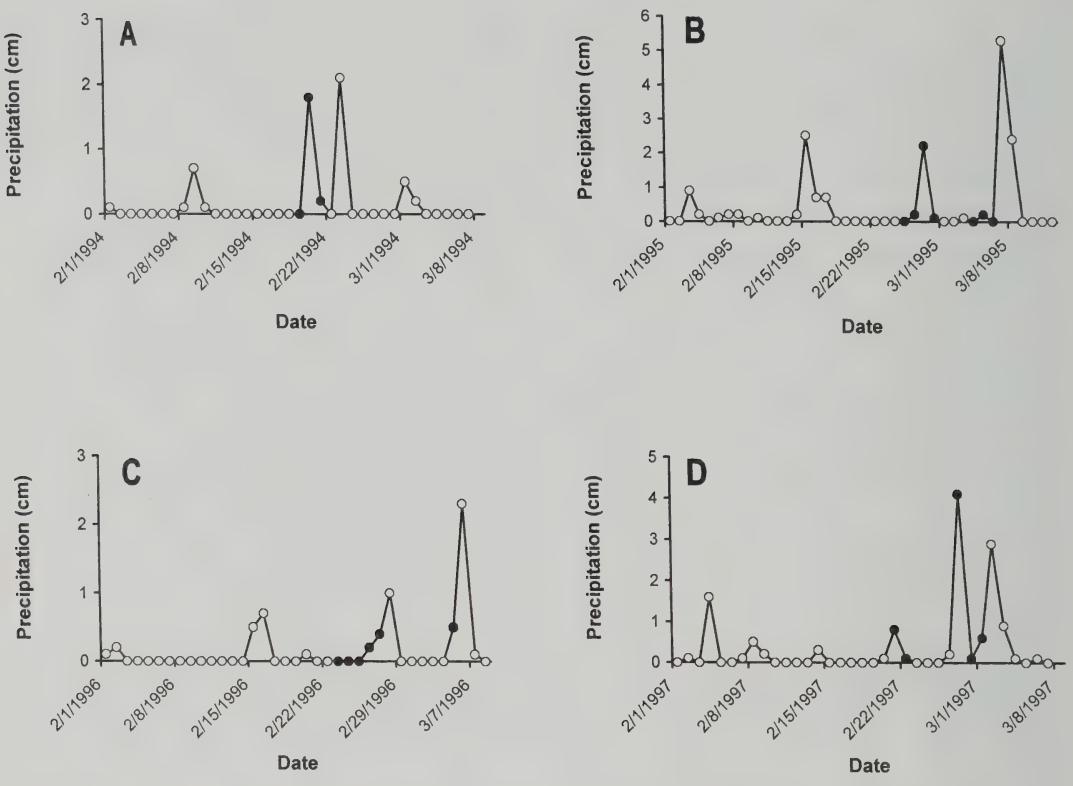


Figure 6. Daily precipitation prior to, during, and immediately following spawning of *Rana sylvatica* at the Pomona/Cave Creek study site, southern Jackson County, Illinois, in the years (A) 1994, (B) 1995, (C) 1996, and (D) 1997. Solid symbols indicate dates when oviposition occurred.

Table 1. Diameters of endosteal bone (EB) and nonremodeled LAGs of *Rana sylvatica* from near Pomona, Jackson County, Illinois.

		Diameter (μm)		
EB/LAG #	N	Mean ± SD	Min	Max
EB	161	196 ± 23.1	165	250
LAG 1	158	279 ± 25.7	240	360
LAG 2	183	378 ± 28.4	310	510
LAG 3	107	433 ± 28.5	360	550
LAG 4	29	477 ± 27.6	400	535
LAG 5	1	540 ± —	540	540

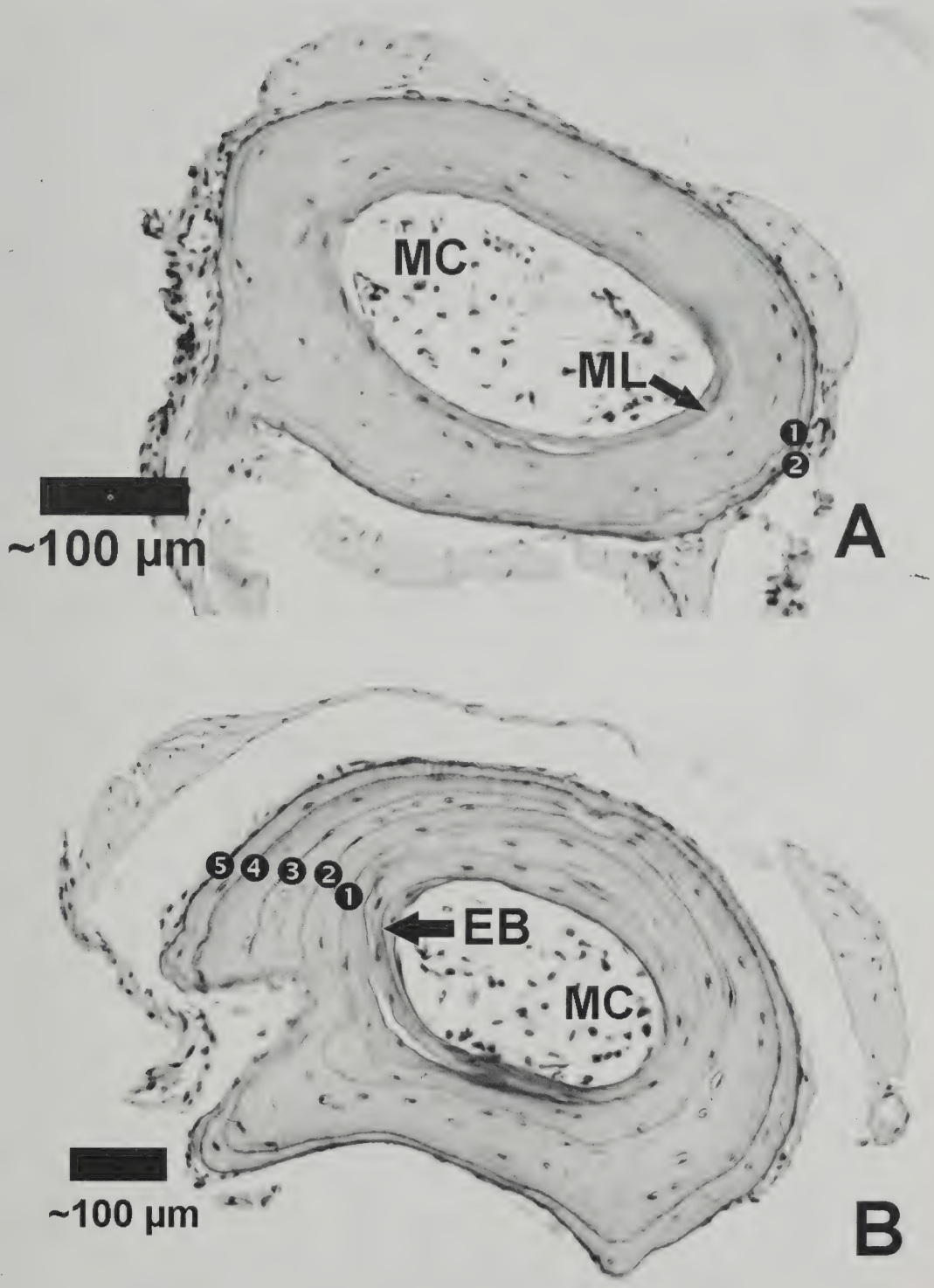


Figure 7. Photomicrographs of hematoxilyn-stained phalangeal cross-sections of *Rana sylvatica* from near Pomona, Jackson County, Illinois. (A) Two-year-old, 44-mm male (magnification = 200X). (B) Five-year-old, 54-mm female (magnification = 160X). MC = medullary cavity, ML = metamorphosis line, EB = limit of endosteal bone, numbers = periosteal lines of arrested growth (LAGs) corrsponding with life year in which LAG was made.

The mean age of males was 2.6 yr (n = 119, SE = 0.07, range = 14, mode = 2) and of females 3.0 yr (n = 69, SE = 0.09, range = 2–5, mode = 3). Mean ages of males and females (Fig. 8) differed significantly (t = 3.6, df = 186, P = 0.0004). The mean SVL of males was 46.1 mm (SE = 0.13, range = 43–50, mode = 46) and that of females 52.2 mm (SE = 0.23, range = 49–57, mode = 53). Mean male SVL (Fig. 9A) was significantly less (t = 25.1, df = 186, p = 0.0001) than mean female SVL (Fig. 9B). There were moderate positive correlations between SVL and ages of males (r^2 = 0.45, P < 0.001) and between SVL and ages of females (r^2 = 0.26, P < 0.001). There was considerable overlap in size between sequential age classes in both sexes (Fig. 10). One-year-old males were 43–45 mm (mean = 43.8) SVL, two-year-olds 43–48 mm (mean = 45.4), three-year-olds 45–50 mm (mean = 46.7), and four-year-olds 46–50 mm (mean = 47.7). Two-year-old females were 49–55 mm

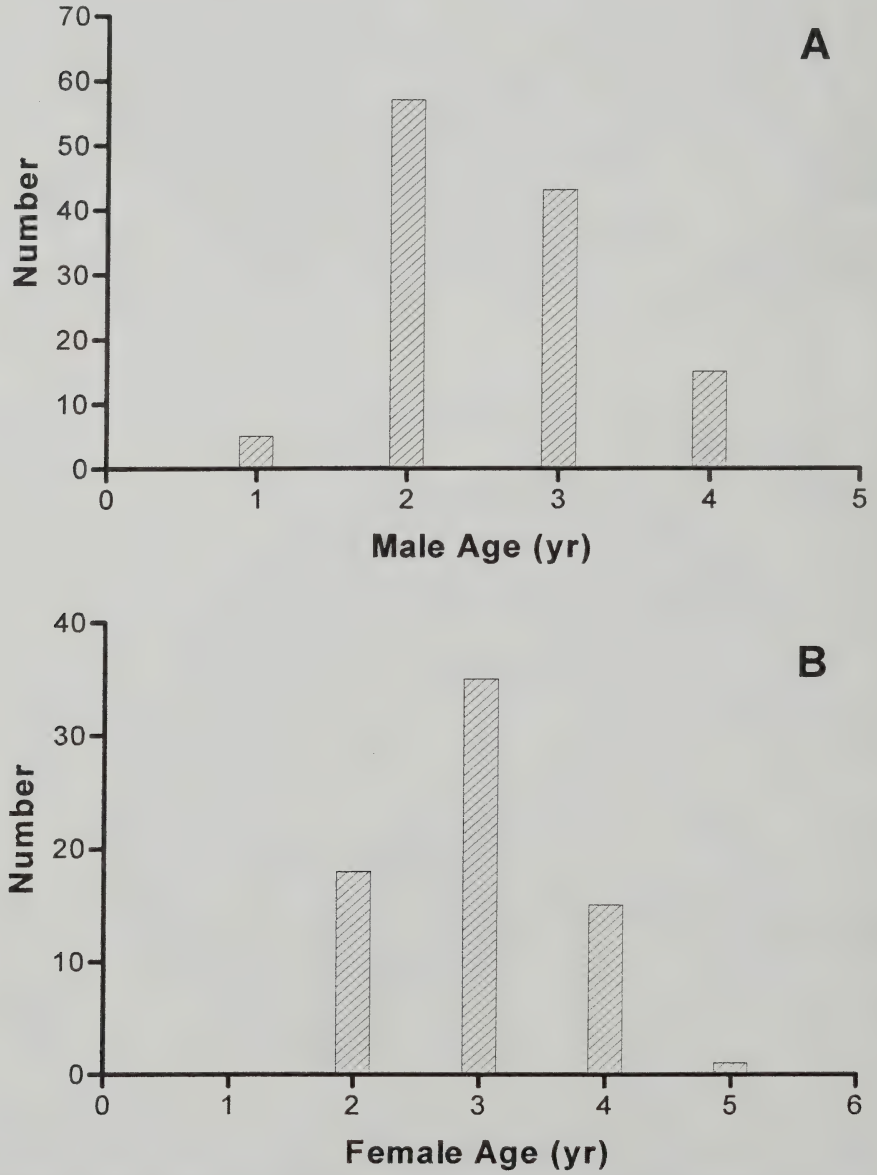


Figure 8. Age-frequency distributions of skeletochronologically estimated age classes of *Rana sylvatica* from a population in the vicinity of Pomona, Jackson County, Illinois. (A) males, N = 119; (B) females, N = 69.

long (mean = 51.3), three-year-olds 49–56 mm (mean = 51.8), four-year-olds 51–57 mm (mean = 54), and a five-year-old was 54 mm. The presence of a few one-year-old males (both in choruses and in amplexus) and two-year-old gravid females indicates that at least some males matured after their first growing season and that some females matured after two years.

There was a low positive correlation between SVLs of mates found in amplexus (r^2 = 0.17, P = 0.01, N = 18) and no correlation between their ages (r^2 = 0.07, P = 0.3, N = 18). Males of all four age classes were found in amplexus with females in the two- to four-year-old age classes. Amplexed pairs included the smallest (49 mm SVL) and largest (57 mm SVL) females observed. The mean SVL (51.5 mm) of amplexed females was not significantly different (P = 0.10) from that of non-amplexed females. Two, three- and four-year-old females were found in amplexus and their

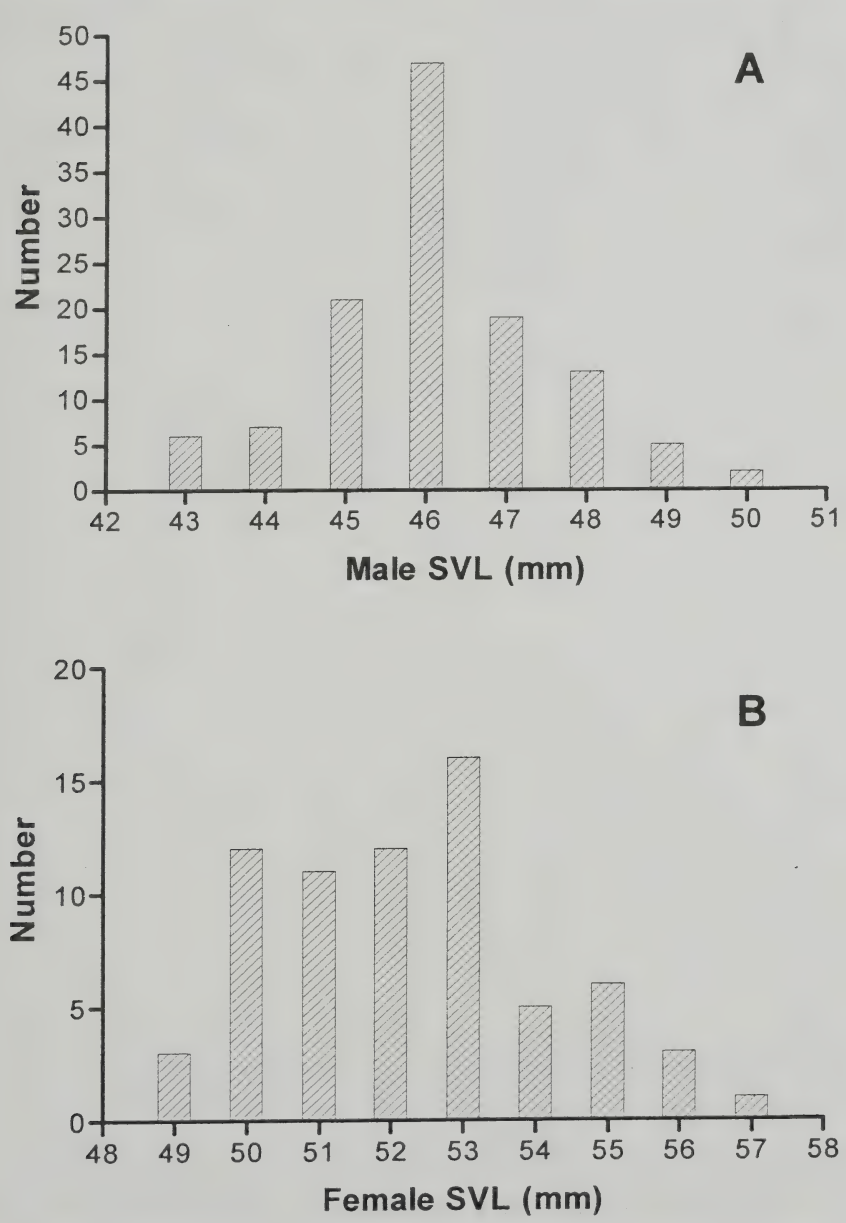
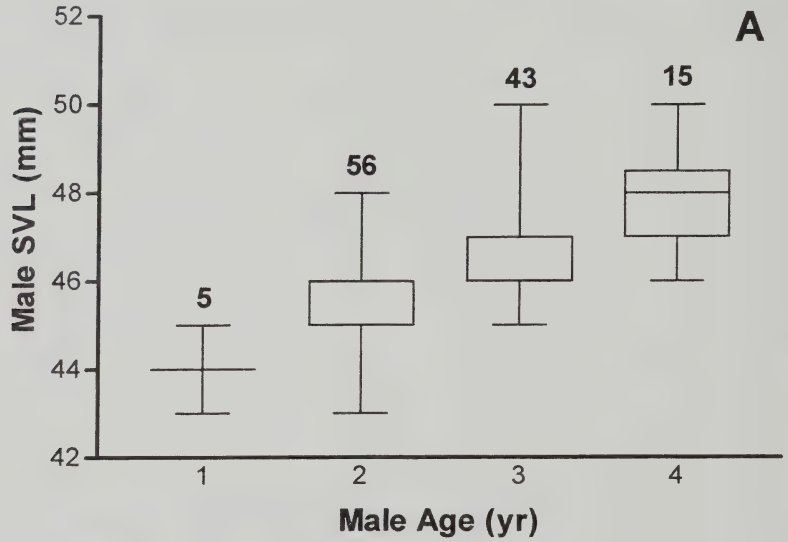


Figure 9. Length frequency distributions of *Rana sylvatica* from a population in the vicinity of Pomona, Jackson County, Illinois. (A) Males, N = 119; (B) females, N = 69.

mean age (2.8 yr) was not statistically different (P > 0.95) from that of nonamplexed females. Males captured in amplexus ranged from the shortest (43 mm SVL) to second-longest (49 mm) observed. The mean SVL (46.1 mm) was not significantly different (P = 0.31) than that of all males. Ages of amplexed males ranged from one to four years old and their mean age (2.4 yr) was not significantly different (P = 0.51) from the mean age of all males.

Clutch Size. Mean size of 24 clutches (15 oviductal and 9 oviposited in the lab) was 575 (SE = 28.08, range = 304–874). Mean ovum/pre-yolk plug embryo diameter was 2.45 mm (SE = 0.04, range = 1.95–2.75). Mean diameter in oviductal clutches was 2.40 mm (SE = 0.06, range = 1.94–2.74) and in oviposited clutches 2.48 mm (SE = 0.07, range = 2.14–2.70). There was strong positive correlation ($r^2 = 0.53$, P < 0.0001, N = 24)



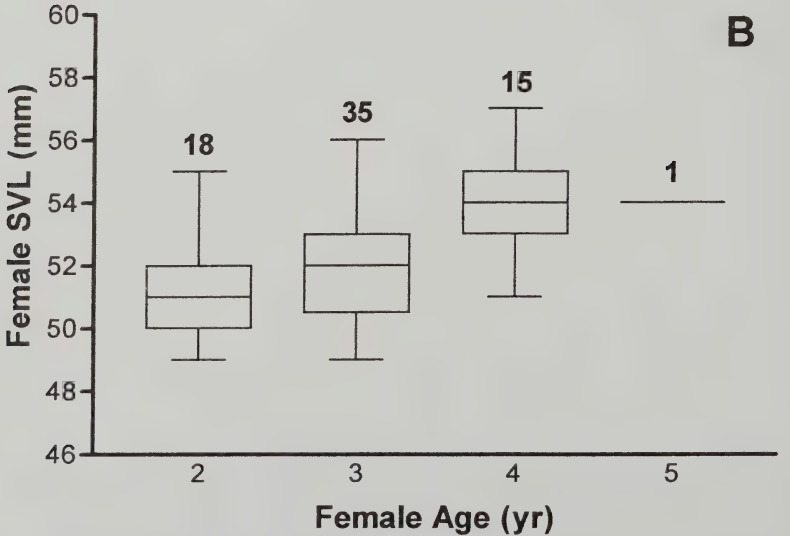


Figure 10. Length-age distributions of *Rana sylvatica* from a population in the vicinity of Pomona, Jackson County, Illinois. (A) Males, (B) females. Key: numbers = sample sizes; extreme upper and lower lateral lines = range of data; upper and lower edges of boxes = interquartile values; lines in boxes = mean values.

between female SVLs and clutch size (Fig. 11A) but no correlation ($r^2 = 0.02$, $P = 0.52$, $N = 24$) between female age and clutch size (Fig. 11B). There were strong negative correlations (overall $r^2 = -0.71$, $P < 0.001$, $N = 24$) between clutch size and mean ovum diameter ($r^2 = -0.67$, $P = 0.002$, $N = 15$) and pre-gastrulation embryo diameter ($r^2 = -0.81$, $P = 0.009$, $N = 9$). All females from which oviductal ova were counted had only granular, non-pigmented or weakly pigmented ovarian ova remaining; thus all mature ova had been ovulated and counted. Only single ova were found to remain in the oviducts of five females that had oviposited.

Other Natural History Notes

Predation on different life-stages was observed on a number of occasions. In each year of the study, egg masses frequently were found hauled out of breeding ponds and left partially

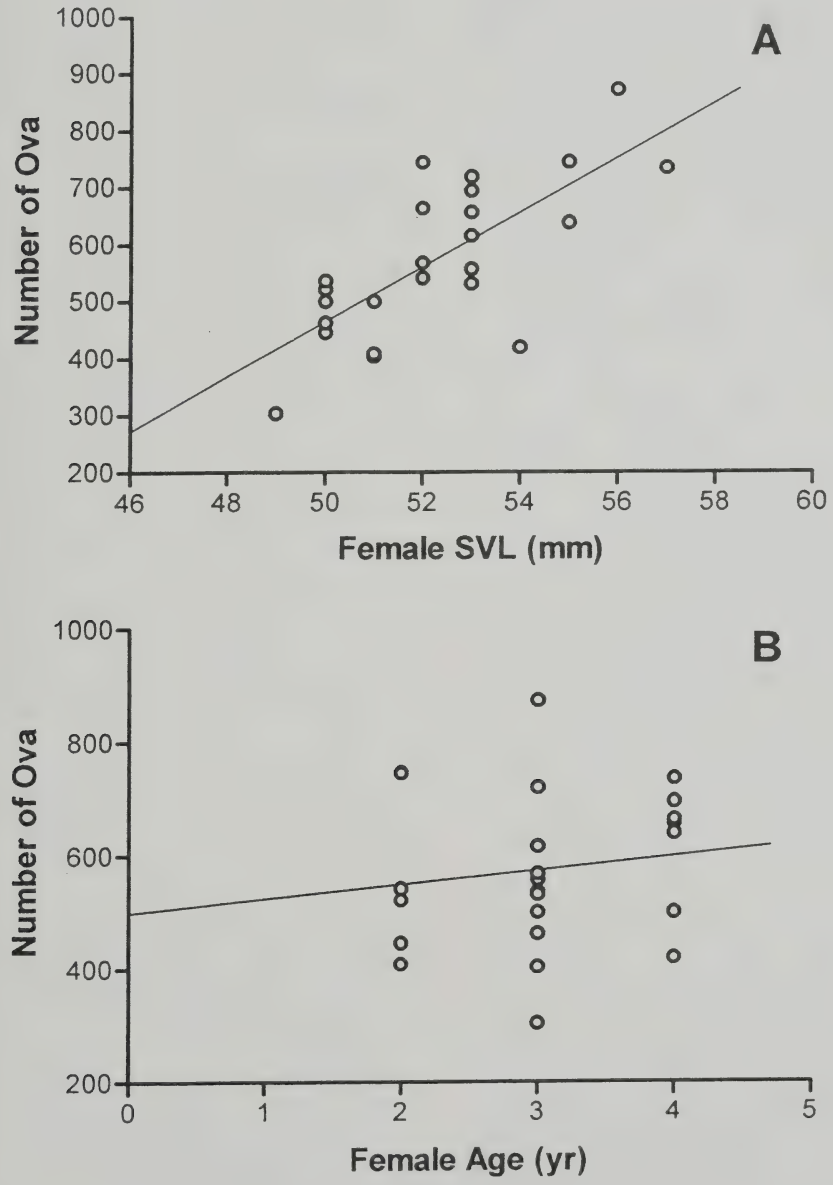


Figure 11. The relationships of (A) length (SVL) and clutch size, and (B) age and clutch size of female *Rana sylvatica* from a population near Pomona, Jackson County, Illinois.

consumed on the banks, probably by raccoons (*Procyon lotor*). In March 1993, marbled salamander (*Ambystoma opacum*) larvae were observed eating eggs from egg masses of *R. sylvatica* and southern leopard frogs (*R. sphenocephala*) oviposited the previous evening. During 1995–1997, *A. opacum* larvae were observed eating *R. sylvatica* tadpoles in a flooded tire-rut. In 1996 and 1997, crayfishes (*Cambarus diogenes* and *Procambarus acutus*) were observed eating eggs from *R. sylvatica* and *R. sphenocephala* egg masses. In 1996, a large *C. diogenes* in a funnel trap (at a drift fence next to a *R. sylvatica* breeding pond) was found consuming a dead gravid female wood frog captured in the same trap. Two other dead adults in the same trap had injuries indicating the crayfish probably had killed them as well. In April 1994, common grackles (*Quiscalus quiscula*), and a garter snake (*Thamnophis sirtalis*) were observed eating *R. sylvatica* tadpoles in shallow tire ruts. In 1995, the stomach of a 78-mm male bullfrog (*R. catesbeiana*) collected at the Cedar Lake pond on the night of peak chorusing by *R. sylvatica* was found to contain a partially digested *P. crucifer* and a freshly consumed, 45-mm male *R. sylvatica*. All of the above predators are well known to opportunistically prey upon various life-stages of amphibians.

Late winter and early spring breeding amphibian species observed breeding in the same SNF ponds (and frequency of occurrence in 30 ponds) as *R. sylvatica* included *Pseudacris crucifer* (73%), *P. feriarum* (83%), *Rana sphenocephala* (57%), *Ambystoma maculatum* (76%), *A. texanum* (53%), and *A. tigrinum* (3%). Other amphibians noted in these ponds, or that bred in them later in the year, included *B. americanus* (13%), *B. woodhousi* (13%), *Hyla chrysoscelis* (50%), *Hyla cinerea* (3%), *R. blairi* (3%), *R. catesbeiana* (13%), *R. clamitans* (39%), *A. opacum* (57%), and *Notophthalmus viridescens* (27%).

On 6 March 1996, a gravid female *R. sylvatica* and male *R. sphenocephala* were found in amplexus in a pond at Cave Creek. No *R. sylvatica* males were heard, and none were observed to oviposit on or after 6 March. The interspecific pair was taken to the laboratory where they remained in amplexus for over 60 h. The female oviposited unfertilized ova after amplexus was ended. Amplexus between these two *Rana* spp. was previously reported by Nelson (1971).

In the laboratory, *R. sylvatica* embryos hatched in 5 to 8 d, and the tadpoles transformed after 47–63 d (mean = 51 d). Numerous metamorphosing frogs were observed at Cave Creek on 19 May 1996 and 10 May 1997, indicating development takes 70–87 d in the wild.

Discussion

Distribution

In Illinois, *R. sylvatica* occurs in forested areas in the state's northeastern corner, east-central perimeter, south to and across the Shawnee Hills, and northwest into Monroe County (Redmer 1998; Smith 1961). There are old museum specimens from JoDaviess and Rock Island counties in extreme northwestern Illinois (Martof and Humphries 1959; Redmer 1998; Smith 1961). A literature record from central Illinois (Garman 1890) was accepted by Smith (1961) but this and another (Blanchard and Princen 1976) not documented by vouchers are questionable (Redmer 1998). Thurow (1994) has been criticized for introducing wood frogs into western Illinois (McDonough County) well outside of the documented range (Redmer 1998; Szafoni et al. 1999).

Previous to this study, *R. sylvatica* was known from few localities in southern Illinois (Redmer 1998). Cagle (1942) stated that this species was uncommon in Jackson and Union counties, and Smith (1961) showed only two records from southern Illinois (from Jackson and Monroe counties). There were later reports from localities in Pope County (Applegate and Zimbleman 1978; Thompson 1972). I documented additional localities in Hardin, Jackson, Pope, Saline, and Union counties (Redmer, 1998; Fig. 2). The apparent distribution gap in the central SNF counties is discussed under "Terrestrial Habitat" (pp. 179–180).

Habitat

Breeding Ponds. In the SNF, *R. sylvatica*

oviposited in a variety of pond types, including a significant number of human-made ones. Colonization of human-made aquatic habitats by amphibians (including *R. sylvatica*) is a commonly reported phenomenon and a variety of such pools or ponds are used (Burkett and Thompson 1994; Cortwright 1998; Stuart and Davidson, 1999) including tire ruts (Adams and Lacki 1993; Camp et al. 1990; Cortwright 1998). Frequent use of human-made aquatic breeding habitat by *R. sylvatica* in the SNF has several conservation implications. These habitats could benefit populations by providing additional oviposition sites. In the Ozark National Forest (Arkansas), Trauth et al. (1989, 1995) reported that most *R. sylvatica* breeding sites were in human-made wildlife ponds. In the SNF, 10% of the ponds I located were mapped as USFS-inventoried wildlife ponds or waterholes.

However, small, human-made aquatic habitats also pose some risks for amphibian larvae. In shallow habitats, eggs or larvae may be vulnerable to insufficient hydroperiod, which could cause total mortality in some years. Although the eggs of *R. sylvatica* can withstand some desiccation caused by temporary terrestrial standing (Forester and Lykens 1988), tadpoles cannot. One SNF tire-rut in which *R. sylvatica* spawned during every year of this study was never deeper than 10 cm when egg masses were in it, and it always dried before tadpoles metamorphosed. Small aquatic habitats (such as tire ruts) may have insufficient food resources for large cohorts of larvae and, thus, fitness, recruitment, or both could be reduced. Most tire-ruts in which *R. sylvatica* oviposited in the SNF were in clay-based roads or trails, and were largely devoid of aquatic macrophytes and other cover. Besides the potential of insufficient food, this could make larvae more vulnerable to predators. Because tire-ruts are usually located on existing trails, they are also prone to disturbance. In 1995 at Cave Creek, an off-road vehicle was driven through a tire-rut that contained 44 fresh *R. sylvatica* egg masses. Several egg masses were damaged or destroyed by tires that rolled over them, and most of the others were covered with silt churned up by the tires as they passed through the water. Other tire tracks in that pool indicated that there was periodic traffic through it in all years of the study. Despite the above factors, tadpoles metamorphosed and left this and one other large tire-rut pond at Cave Creek in 1996 and 1997 (the only years they were monitored during metamorphosis), so these must provide adequate aquatic habitat in some years.

The frequency of ponds in closed-canopy sites (70%) vs. open sites (30%) in the SNF is similar to that reported from Michigan (Werner and Glennemeier 1999) where *R. sylvatica* tadpoles hold a competitive advantage over sympatric *R. pipiens* and *B. americanus* under closed canopies.

Terrestrial Habitat. Although the range of *R. sylvatica* is mostly boreal, this species has been reported from a variety of habitats including tundra, subalpine woodlands, willow thickets, wet meadows, bogs, and coniferous, deciduous, and other temperate forests of various canopy species (Behler and King 1979; Conant and Collins 1998; Hammerson et al. 1986; Harding 1997; Martof 1970; Martof and Humphries 1959; Oldfield and Moriarty 1994; Russell and Bauer 1993; Trauth et al. 1995). The Shawnee Hills Natural Division is characterized by non-glaciated hills underlain by limestone or sandstone bedrock and covered with loess soils. Most of the division was heavily forested during presettlement times (Schwegman 1973). Uplands are dominated by oak-hickory forests while more mesic ravines contain mixed oak-beech-tulip poplar-maple forest, and the floodplain forests consist of these species and sycamore, ash, and box elder (Schwegman 1973; Voigt and Mohlenbrock 1964). The Ozark Natural Division is part of the Ozark Plateau. It is characterized by dry loess soils over limestone bedrock and forests of somewhat similar composition to the Shawnee Hills. The flora is characteritic of the Ozarks, but otherwise this division has much natural similarity to the Shawnee Natural Division (Schwegman 1973).

The lack of records of *R. sylvatica* from the center of the Shawnee Hills Division and from the Cretaceous Hills Section of the Coastal Plain Natural Division is interesting. I

searched many human-made wildlife ponds in these areas but found no wood frogs. The forest habitat appeared suitable and egg masses of *Ambystoma maculatum* (a species that commonly breeds in the same ponds as *R. sylvatica* elsewhere in the SNF) were abundant in these ponds. Johnson County and the eastern Cretaceous Hills receive more precipitation than any other part of Illinois (Schwegman 1973), so it is unlikely that lack of moisture precludes *R. sylvatica* from these areas. However, while forests of the Cretaceous Hills are similar in species composition to those of the Shawnee Hills Natural Division, the soils (composed of tertiary sands, gravels, and clays) differ (Schwegman 1973). Also, woodlands in the Cretaceous Hills are interspersed with dryer barrens communities that are characterized by floras more often associated with prairie outliers or woodlands of the southeatsern United States (Stritch 1987). The distributions of two plethodontid salamanders (two-lined salamander, *Eurycea cirrigera*; zigzag salamander, *Plethodon dorsalis*) have some similarities to that of *R. sylvatica* in the SNF. *Eurycea cirrigera* is common in rocky, wooded stream valleys in Saline, Hardin, Gallatin, and northern Pope counties, but in the Cretaceous Hills it is documented only from one disjunct population in a few ravines in southeast Pulaski County and seems to be absent from the hills of southern Pope County (Mierzwa 1989). Like *R. sylvatica*, *P. dorsalis* occurs in two apparently disjunct populations separated by the central Shawnee Hills (Smith 1961), although it is common in the Cretaceous Hills in Pope County (Redmer pers. obs.). It is possible that the currently known wood frog and zigzag salamander populations in the eastern and western SNF may not be disjunct at all, but simply remain undiscovered in the intervening area. Until recently, there were so few wood frog records in the SNF that despite the recent records, microdistribution remains poorly known. Additional surveys for tadpoles following the breeding season could find additional localities.

I observed few *R. sylvatica* after the breeding season, and have little data on habitat use. My only observations after the breeding season were nocturnal encounters (frogs on roads) and two individuals in shaded ravines. D. Corgiat (pers. comm.) conducted extensive field studies of the golden mouse (*Ochrotomys nuttali*) in the Cave Creek valley, and was familiar with *R. sylvatica* but never encountered one after the breeding season. E. Ulaszek (pers. comm.) found individuals buried in deep, cool accumulations of leaves in shaded rocky ravines in the SNF during summer. Thompson (1972) found individuals on wooded hillsides around Little Lusk Creek (Pope County). In Arkansas, wood frogs occur …[near the mouths of caves and bluff crevices] following the breeding season (Trauth et al. 1995:47). Adults from southern populations have higher critical thermal maxima (CTM) then nonacclimated individuals from more northern populations but there is no difference in tolerance to low temperatures (Lotshaw 1977; Manis and Claussen 1986). Southern wood frogs have CTM temperatures of 34.2°–36.8°C (Lotshaw 1977; Manis and Claussen 1986). Daily high temperatures in southern Illinois often reach or exceed this range in summer. Either this species must have adaptations to survive hot southern Illinois summers or perhaps soil temperature in closed-canopy woodlands remains cool enough to provide refuge then. Heatwole (1961) reported that *R. sylvatica* sought refuge under leaf litter as ground humidity decreased. Observations of nocturnal activity and presence of individuals in cool microhabitats indicate that southern wood frogs are active during cool periods or seek refuge in cool habitats during warm weather. Further study of the summer habitat and movements in southern Illinois (or elsewhere near the southern edge of its range) could add to the understanding of mean physiological longevity of this species (see "Demography" section pp. 181–186).

Population Studies

Breeding Phenology. *Rana sylvatica* usually is reported to have an explosive breeding season (Herreid and Kinney 1967; Howard 1980; Meeks and Nagel 1973; Seale 1982). It was explosive in all five years that I studied this species at Cave Creek and Cedar Lake.

Air temperatures at which breeding took place in the SNF varied, but generally were similar to those reported elsewhere (Herreid and Kinney 1967; Howard 1980; Meeks and Nagel 1973; Seale 1982; Wright and Wright 1949). *Rana sylvatica* is known to hibernate terrestrially near the soil surface (Bellis 1962; Heatwole 1961; Howard 1980; Licht 1991; Schmid 1982; Storey 1984; Storey and Storey 1987; Zweifel 1989). As an adaptation to the effects of freezing winter temperatures, this species is somewhat resistant to dehydration (Schmid 1965) and produces physiological cryoprotectants (Storey 1984; Storey and Storey 1987). At Cave Creek, breeding occurred with rising soil temperatures. In three of five years, breeding was interrupted by cold air temperatures but resumed immediately when air temperatures re-warmed (Fig. 3). In these instances, soil re-warmed more slowly, and did not reach 9°C before breeding resumed (Fig. 4). While freeze tolerance may persist for some time after emergence from hibernation (Storey and Storey 1987), not all wood frogs returned to terrestrial dormancy after reaching the ponds. Some were observed resting on pond bottoms, while others were partially hidden under sunken leaves during cold nights in 1995 and 1996. It is likely that most adults already in the ponds when air temperatures dropped did not leave, and they resumed breeding after air and water temperatures rose sufficiently. Similar observations have been made elsewhere (Davis and Folkerts 1986; Meeks and Nagel 1973; Trauth et al. 1995). Post-emergent wood frogs can survive at least 10 days submerged in water under a frozen surface (Licht 1991).

As would be expected of a species with a broad latitudinal range, and in which breeding is triggered by temperature, breeding of *R. sylvatica* is somewhat predictable along a south to north gradient (Guttman et al. 1991). Considering latitude and year-to-year variation in weather, the dates at which breeding occurred in the SNF were comparable to dates reported elsewhere in the southern portion of its range (Table 2).

Demography. Two previous studies (Bastien and LeClair 1992; Sagor et al. 1998) used skeletochronology to estimate age in populations of *R. sylvatica*. Both examined samples of phalangeal cross-sections from populations in southern Quebec, Canada, and both detected LAGs. Bastien and LeClair (1992) estimated that LAG 1 was obliterated by endosteal remodeling in up to 29% of individuals. Sagor et al. (1998) estimated that LAG 1 was obliterated in 6% of individuals. In my sample, endosteal remodeling partially obscured LAG 1 in 11% and completely obliterated it in 4% of phalanges.

Studies by Berven (1982a,b; 1988) and Berven and Gill (1983) documented geographic variation in life history and demographic traits of *R. sylvatica*. Growing season and elevation affect body size in this species (Berven 1982a,1982b, 1988; Berven and Gill 1983; Davis and Folkerts 1986; Martof and Humphries 1959; Sagor et al. 1998). Snout-vent lengths have been reported from a number of localities in the southern part of the range (Table 3). The only previous size data on Illinois specimens were given by Smith (1961), who found SVL to be greater in the southern part of the state than in the northeast corner. The largest SVL I observed in a Jackson County sample (a 57-mm female) was greater than the maxima of all of Smith's samples from Illinois.

Body size and age at maturity are environmentally plastic traits in some amphibians (Augert and Joly 1993; Berven 1981, 1982a; Scott 1994; Tilley 1973, 1980). Several studies have reported ages of individual *R. sylvatica* (Table 4). The proportions of age classes in southern Illinois are most similar to those reported from Quebec, Canada, by Bastien and LeClair (1992), who also estimated age from skeletochronology. They obtained mean ages of 2.8 yr (range = 2–4) for males, and 3.2 yr (range = 2–5) for females, compared with 2.6 and 3.0 yr in southern Illinois. In southern Illinois some males matured by the beginning of their second year and females by the beginning of their third year. Elsewhere, males have been reported to mature in 1–3 yr and females in 2–4 yr (Bellis 1962; Berven 1982a; Bastien and LeClair 1992, Sagor et al. 1998). Sexual differences in age at maturity have also been reported in other *Rana* as well (Ryser 1988, 1996; Shirose and Brooks 1995).

Table 2. Earliest reported dates (d/m/y) of *Rana sylvatica* breeding activity in the southern part of the species' range.

Source	Location (Approximate Latitude)	Date
Berven (1982)	Lowland Maryland (38°N)	15/02/76
	Mountain Virginia (38°N)	28/02/76
Camp et al. (1990)	N Georgia (35°N)	12/02/87
Davis and Folkerts (1986)	E Alabama (33°–34°N)	21/02/79
		17/01/80
Guttman et al. (1991)	EC Missouri (38°N)	26/02/87
Meeks and Nagel (1973)	E Tennessee (36°N)	22/02/71
Redmer (this study)	Jackson Co., Illinois (37°N)	17/03/93
		19/02/94
		27/02/95
		26/02/96
		22/02/97
Trauth et al. (1989, 1995)	N Arkansas (36°)	07/02/87
		01/02/88
		25/01/89
		01/02/90
		02/02/91
		31/01/92

Table 3. Reported sizes (SVL) of *Rana sylvatica* from the southern part of the species' range.

			Males		Females	
Source	Location	Maximum (mm)	Mean (mm)	Range (mm)	Mean (mm)	Range (mm)
Berven (1982a)	Maryland (lowland)	—	41.7	—	47.7	—
	Virginia (mountain)	—	55.3	—	64.4	—
Davis and Folkerts (1986)	Alabama	—	50.0	—	60.0	—
Guttman et al. (1991)	Missouri	67	51.1	42–62	60.3	48–67
Martof and Humphries (1959)	Georgia & Carolinas	—	54.8	—	66.8	—
Meeks and Nagel (1973)	Tennessee	75	57	55–63	69	63–75
Minton (1972)	N Indiana	52	38.4	35–42	43.8	38.5–52
	S Indiana	62.5	43.8	43–54	52.8	41–62.5
Redmer (this study)	Jackson Co., Illinois	57	46.1	43–50	52.2	49–57
Smith (1961)	SW Illinois	50.8	—	—	—	—
	EC Illinois	54.4	—	—	—	—
	NE Illinois	49.3	—	—	—	—
Trauth et al. (1995)	Arkansas	76.7	55.1	46–65.1	65.6	59.9–76.7

Table 4. Age structure (percent frequency) in populations of *Rana sylvatica*.

Source	Location	Age	Males	Females
Berven (1982a)*	Maryland	1	86.0	1.1
	(low elevation)	2	14.0	98.9
		3	0	0
	Virginia	1	0	0
	(high elevation)	2	13.6	0
		3	83.7	44.2
		4	2.7	55.8
Bastien and LeClair (1992)	Quebec	1	0	0
		2	32.1	8.7
		3	53.6	69.6
		4	14.3	13.0
		5	0	8.7
Redmer (this study)	S. Illinois	1	4.2	0
		2	47.5	26.1
		3	35.8	50.7
		4	12.5	21.7
		5	0	1.5
Sagor et al. (1998)	Quebec	1	4.1	0
		2	49.0	45.5
		3	40.8	33.8
		4	6.1	21.2

*Ages at maturity.

An alternative to expressing mean longevity in years is mean physiological longevity (MPL = mean age in years multiplied by the average number of frost-free days in the region). Bastien and LeClair (1992) commented on possible variation in MPL of different wood frog populations. From theirs and other published data (Berven 1982a), they calculated MPL for three populations (Quebec, Maryland, and Virginia). Assuming 195 frost-free days for southeastern Jackson County (Schwegman 1973), the MPL of wood frogs is much greater in Jackson County than those calculated for other populations (Table 5) by Bastien and LeClair (1992). They speculated that MPL was relatively constant in females but geographically more variable in males, and that earlier maturity curtailed the potential life span of males. Considering the greater MPL of Pomona wood frogs (both males and females), the former does not appear to be the case in southern Illinois. Local environmental factors (i.e., larval density, size and fitness at metamorphosis) may contribute to considerable plasticity in growth and longevity, as well as the timing of and size at sexual maturity in amphibians (Berven 1988, 1990; Berven and Gill 1983; Scott 1994; Tilley 1973, 1980). Numerous studies of factors influencing mate selection in anurans have been conducted (Berven 1981; Fellers 1979; Halliday 1983; Howard 1978, 1980, 1983; Howard and Palmer 1995; Howard et al. 1994; Howard and Kluge 1985; Lykens and Forester 1987; Ryan 1980). In some species, large females mate more frequently with large males (Duellman and Trueb 1986; Halliday 1983; Howard and Kluge 1985; Ryan 1980). Because large males often are thought to be the oldest males and have a history of reproductive success, they might advertise fitness (through physical characteristics of vocalization or other cues) and be more attractive to females (Lykens and Forester 1987; Ryan 1980). However, despite previous assumptions that females probably choose mates, most studies have indicated that this occurs in only a minority of anurans (Halliday 1983).

The lack of correlations between *R. sylvatica* mate SVL and mate age in the SNF suggests that mate selection is not strongly related to either variable. Previous studies of mated *R. sylvatica* (Berven 1981; Howard 1980; Howard and Kluge 1985) found non-random pairing in which larger males had a reproductive advantage over smaller ones because once in amplexus larger size and limb length allowed males to amplex longer and more easily defend their mates from challenges by smaller males. To date, there is no evidence of mate choice by female wood frogs. In the SNF, older and larger adults were statistically no more likely to mate than younger and smaller ones. Berven (1981) found no correlations ($r^2 = 0.05$ and 0.08) between male and female sizes in mated pairs in two Maryland ponds, and a low positive correlation ($r^2 = 0.16$) in a third pond. He

Table 5. Comparison of mean age and mean physiological longevity of *R. sylvatica* from Quebec (Bastien and LeClair 1992), Maryland (Berven 1982a), Virginia (Berven 1982a), and the Shawnee National Forest (this study).

	Quebec		Maryland		Virginia		SNF	
Parameter	M	F	M	F	M	F	M	F
Mean age	2.8	3.2	1.7	2.4	3.6	3.8	2.6	3.0
Frost-free days	130	130	177	177	121	121	195	195
Physiological longevity (d)	364	416	290	421	438	458	507	585

suggested that male-male competition and mate choice by males occur in *R. sylvatica*. I and others (Berven 1981; Howard 1980; Phillips and Wade 1990) have observed competition for females by males that attempted to dislodge each other from amplexed females. Several males often attempt to amplex the same female. Amplexus by multiple males sometimes leads to female mortality (Howard 1980; Phillips and Wade 1990), although I did not observe this in the SNF. Smith-Gill and Berven (1980) found that larger (probably older) males produced more sperm and thus have greater reproductive potential than smaller males, so offspring of females that mate with larger males should be at a selective advantage. *Rana sylvatica* usually is described as an explosive synchronously breeding species with males and females arriving at breeding ponds simultaneously and completing oviposition in a few days (Berven 1981; Howard 1980; Phillips and Wade 1990; Trauth et al. 1989, 1995). This is true in southern Illinois.

Clutch Size. Studies of anuran fecundity generally have shown a negative correlation between clutch size and ovum diameter and a positive correlation between female size and clutch size (Berven 1988; Duellman and Trueb 1986; Salthe and Duellman 1973; Salthe and Mecham 1974). The positive correlation between body size and age implies a positive correlation between clutch size and age as well (Duellman and Trueb 1986). However, in some species considerable reproductive variation among populations, or among females in the same populations, has been reported (Berven 1982b, 1988; Crump 1984; Dushane and Hutchinson 1944; Kaplan 1980; Pettus and Angleton 1967).

Clutch sizes of *R. sylvatica* in southern Illinois are within the ranges reported elsewhere in the southern part of the range (Table 6). Single eggs were found in the oviducts of five spawned females, so it is likely that nearly all oviductal ova were oviposited and yolked ovarian or oviductal ovum compliments are validly used as measures of fecundity. Some older studies (Minton 1972; Mount 1975; Pope 1944; Smith 1961; Wright and Wright 1949) have reported a general range of 1,000 to 3,000 eggs per clutch. More recent studies in the southern part of the range have consis-

Table 6. Reported clutch sizes and ovum diameters in *Rana sylvatica* from the southern part of its range.

		Clutch Size		Ovum Size (mm)	
Source	Location	Mean	Range	Mean	Range
Berven (1982a)	Maryland (low)	642	642 ± 200[1]	1.8	1.83 ± 0.29[1]
	Virginia (mountain)	920	920 ± 217[1]	2.3	2.28 ± 0.13[1]
Camp et al. (1990)	Georgia	553	295–706	2.8	2.2–3.3
Davis & Folkerts (1986)	Alabama	496	350–709	2.9	—
Meeks & Nagel (1973)	Tennessee	465	386–543	2.3	2.1–2.4
Redmer (this study)	Jackson Co., Illinois	575	304–874	2.5	1.95–2.75
Trauth et al. (1989)	Arkansas	883	510–1433	2.8	2.2–3.3

[1] Ranges are ± standard deviation from mean.

tently reported smaller clutches (range = 295–1,433; Table 6).

Adult *R. sylvatica* are well known to have physiological adaptations to cold (Layne and Lee 1987; Lotshaw 1977; Storey 1984; Storey and Storey 1987). In addition, thick, insulative egg envelopes, large ova, and communal oviposition have been reported as adaptations that protect embryos from low temperatures that occur suddenly during the breeding season (Howard 1980; Seale 1982; Waldman 1982; Waldman and Ryan 1983). Larger eggs are more resistant to desiccation caused by terrestrial stranding (Forester and Lykens 1988). Ovum diameters (mean = 2.5 mm, range = 1.95–2.75) in the SNF are within the range of diameters reported from other southern populations (Table 6). Because oviposition in the SNF usually took place in late February when there was still a risk of cold weather that could freeze ponds, large ova may be a necessary adaptation to cold weather there as well.

In the SNF, wood frog clutch and ovum sizes collected in 1995 and 1996 were negatively correlated. This follows a pattern reported previously from other amphibian species (Kaplan 1979, 1980; Kaplan and Salthe 1979; Salthe and Duellman 1973). Numerous studies of reproductive investment in amphibians (and other organisms) have examined the trade-off between number and size of offspring (the model of "optimal parental investment" [Smith and Fretwell 1974]). There is considerable evidence that environmental factors greatly influence these traits (Berven 1988; Crump 1981, 1984; Crump and Kaplan 1979; Kaplan and King 1997; Kuramoto 1978). In *R. sylvatica*, environmental factors affect traits such as female age and size, which may in turn affect clutch and ovum size (Berven 1988). However, in 1995 and 1996, the SVL of SNF female *R. sylvatica* was strongly correlated with clutch size, but female age was not (Fig. 11). While the reasons for this are beyond the scope of this study, this is interesting because in my sample female age and SVL were positively correlated.

Other Comments. Age and size structure and reproductive characteristics of adult amphibians may be influenced strongly by variation in larval survival and recruitment (Berven 1990; Miaud et al. 2000; Semlitsch et al. 1996). In amphibians, ovum size, competition, growth rate, and mass at metamorphosis are known to contribute to larval fitness and recruitment of metamorphs (Berven and Gill 1983; Berven 1988, 1990; Parris and Semlitsch 1998; Semlitsch and Pechmann 1988; Smith 1987). Significant geographic variation in life history and reproductive traits of *R. sylvatica* has profound effects on local population dynamics (Berven 1982a,b; Berven 1988; Berven and Gill 1983). Future regional studies or monitoring efforts designed to include this and other wide-ranging amphibians should continue to investigate or account for how these factors regulate adult populations. Skeletochronology has been shown to be an effective method for obtaining age estimates for many species of amphibians. However, when used in single years, this technique reveals nothing about population trends. It should be used over several years to detect fluctuations in age structure among years (Friedl and Klump 1997). Regional studies of amphibian populations should combine methods (such as skeletochronology) for determining demography of adult populations with studies of reproductive traits and relationships between larval and adult life stages. Such comprehensive studies may be more useful for tracking regional trends in amphibian populations, and could potentially help to identify reasons contributing to regional rarity or declines of some species.

Summary

The wood frog (*Rana sylvatica*), an uncommon species in Illinois, was studied in the Shawnee National Forest in the extreme southern part of the state. Frogs were documented from 20 localities in 5 counties (Jackson, Hardin, Pope, Saline, and Union) in the Shawnee Hills and Ozark Natural Divisions. Eggs or tadpoles were observed in 30 aquatic breeding sites, including ephemeral ponds and depressions, semi-permanent ponds, human-made ponds, roadside ditches, and ruts (caused by vehicles) in dirt trails. Surrounding

habitat included floodplain and upland deciduous, coniferous, and mixed deciduous/coniferous forests. One population, which bred in at least 13 ponds or flooded depressions in southern Jackson County, was studied more intensively between 1993 and 1997. Explosive breeding took place in this population in late winter and coincided with surface soil temperatures of 9°C, and less so with warm rains and specific air temperatures. Skeletochronologically estimated age of breeding adults was compared to SVL, fecundity, and by mate data (SVL and age). There were moderate positive correlations between ages and SVLs of males and of females. There were no correlations between ages and SVLs of amplexed mates. Clutch size was more strongly correlated to female SVL than to female age, and mean ovum diameter was negatively correlated to clutch size.

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Illinois Natural History Survey
Natural Resources Building
607 East Peabody Drive
Champaign, Illinois 61820
217-333-6880

A Division of the Illinois Department of Natural Resources